

The University of Chicago

DEVELOPMENTAL MORPHOLOGY OF
ALLIUM CEPA

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1933

By
CHARLES ANDREW HOFFMAN

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DEVELOPMENTAL MORPHOLOGY OF ALLIUM CEPA

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CHARLES ANDREW HOFFMAN

(WITH TWENTY-NINE FIGURES)

Introduction

Of all the Liliaceae, the onion, *Allium cepa* L., is of greatest economic importance. Its distribution is world-wide and its popularity as an article of food is almost as extensive. SACHS (10), in a well illustrated article, discusses the microchemistry of the seed and seedling, together with the anatomy and germination of the seedling. SIDERIS (11) notes that onion roots emerge in two sets, one group for the early life of the seedling and another for bulb formation. The first roots die as the second group becomes functional. JONES and BOSWELL (5) found that the primordia of the flower axis in bulbs which were formed the previous season are differentiated during March. POESE (8) notes that the vascular bundles in all the Liliaceae he investigated fluctuate between a collateral and a concentric type, the latter appearing most commonly in the rhizome and at the nodes. MANGIN (6) states that the meristem giving rise to adventitious roots is absent in all monocotyledons without these roots.

MATERIAL AND METHODS.—In the fall of 1930 and in the following summer, material was grown from pedigreed seed of the Yellow Globe Danvers onion. From this material the various stages to be studied were selected. All the material, except the primary roots which were killed in Flemming's medium fluid, was killed in a mixture of four parts absolute alcohol and one part glacial acetic acid, passed through five mixtures of ethyl and butyl alcohol, and finally imbedded in paraffin as described by ZIRKLE (13). The primary roots were cut 6μ thick and the other material from 8 to 15μ thick.

Embryo

The mature embryo is a curved cylinder about 0.4 mm. in diameter and 6 mm. long, of almost uniform width, somewhat pointed

at the hypocotyledonary end and rounded at the opposite or haustorial end. It is almost completely surrounded by an endosperm whose cells contain fat (10), and whose walls are much thickened with a hemicellulose which on hydrolysis yields mannose (2). The haustorial end may be merely curved at right angles to the remainder of the embryo or may form more than a complete circle. A 270° arc is the average. About one-tenth of the length of the embryo is hypocotyl; the rest is cotyledon. Proximal to the tip of the hypocotyl, a distance twice the diameter of the embryo, is a slit in the cotyledon or first leaf through which the second leaf grows. This slit and the cavity inside it are usually filled with a waxy or gummy substance. The cavity thus formed by the hollow base of the cotyledon surrounds the primordium of the second leaf, which usually is tongue-shaped, with a length about twice its thickness. The slit, according to SACHS (10), occurs with equal frequency on the concave and on the convex sides of the embryo.

All of the cells of the embryo are very thin walled. The five regions of the embryo as seen in longisection and described by SACHS are clearly distinguishable. They are: (1) the peripheral layer, which a week after planting has formed the epidermis of the cotyledon together with its stomata and guard cells; (2) the parenchyma of hypocotyl and of cotyledon which, even in the embryo, has many intercellular spaces; (3) the single procambial strand running from the promeristem of the root tip to the stem region and up through the cotyledon to the peripheral layer of the haustorial portion. The cells of this procambial strand and of the parenchyma are in long rows. In some embryos the procambial strand contains spiral elements which are first differentiated above the region of the stem, a distance two or three times the diameter of the embryo; (4) the promeristem of the root and of the stem tip; (5) the root cap.

Germination

SACHS' account of the changes which occur in the form of the embryo and in the content of the cells during germination was confirmed. Development of the embryo begins with elongation of the lower and middle regions of the cotyledon. Within 24 hours the hypocotyl is pushed through the seed coat and soon thereafter most

of the cotyledon also is pushed out. The tip of the cotyledon, however, remains imbedded in the endosperm of the seed from which it absorbs food. When 4-6 mm. of the embryo is outside the seed coat, a bending in the cotyledon occurs above the slit so that the hypocotyl is directed downward. By the end of a week the root has grown downward 4-6 cm., while the short stem region has remained at about the same level as that occupied by the seed at the time of planting, and the cotyledon has attained a length of 8-12 mm. In the cotyledon, midway between the slit and the attached seed, a region has become sharply bent double so as to present its convex side to the soil surface above it. This is the soil-penetrating organ or "knee," which is carried upward by elongation of the part of the cotyledon on either side of it.

Apparently there is no localized meristematic region in any part of the cotyledon, cell divisions occurring throughout its entire length, although the cells at each end reach their full size later than the others. After becoming vacuolate and six to eight times their embryonic length, the cells of the cotyledon divide not more than two or three times and elongate slightly. During the first five days no mitotic figures are found in the cotyledon, the growth being due to cell enlargement alone. A few days later figures become abundant but two weeks later are absent. Mitoses occur in all tissues but last to begin is the region near the seed. After eight or ten days, elongation of the seed limb of the cotyledon ceases, while the stem limb, especially near the stem region, continues to elongate slightly. This causes the stem limb to be curved and the seed limb to be stretched across the curve like a bowstring. By this time the haustorium has absorbed so much of the endosperm that it lies loosely in it, and, under the growth tension of the cotyledon, the haustorium is pulled out of the seed and germination is completed. At this time the cells in the concave side of the knee grow until finally the seed limb of the cotyledon also points upward, although a bend always marks the location of the knee. The haustorium, once out of the seed, immediately withers but the rest of the cotyledon remains photosynthetic.

By the time germination is completed the primary root has attained almost its full length of 10-12 cm. It does not branch, and all subsequent roots originate adventitiously from the stem. Just

above the region of root hairs at the top of the hypocotyl the first two or three adventitious roots push out through the outer cortex of the lower stem. This action seems to be both lysigenous and schizogenous. These roots originate from the parenchyma of the inner cortex, which becomes meristematic (fig. 11). The first of these roots arises from the cortical sector below the slit. The next appears usually more than 90° to the right or left of the first, and if there be a third, it is developed in the region diametrically opposite the second. Subsequent adventitious roots originate as does the first. There is no regularity in the order or place of their appearance. Each successive root is usually less than half its own diameter above the previous one. A plant five months old may have had well over 100 root primordia and roots.

Primary root

The primary root is an exarch radial protostele, usually diarch but sometimes triarch. When both xylem and phloem are mature there is no parenchyma in the stele except the uniseriate pericycle. The central metaxylem consists of one to five, usually two, larger elements which mature into scalariform vessels (fig. 9). Casparian strips are apparent in a seedling six days old, but never become very thick. Cortex and epidermis are parenchymatous.

Development of the root axis is like the "type 2" of JANCZEWSKI (4) as modified by TREUB (12). The meristem consists of two regions, the one giving rise to the plerome and the other to the periblem, epidermis, and root cap (fig. 15).

As seen in longisection the stele appears to arise from two, three, or four cells at its distal end. From the derivatives of these a pericycle is first differentiated, and then one of the centrally located cells enlarges and thereafter does not divide so often as those surrounding it but grows in all dimensions, especially longitudinally. From a row of such cells the large central vessel is formed. One or two periclinal divisions of the surrounding cells bring the stele to its diameter of five to ten, usually seven, cells. Subsequent cell divisions take place transversely and thus longitudinal growth continues. The cells of the pericycle are slightly shorter than those of the endodermis and neighboring cortical cells, but are more easily distin-

guished because they are immediately outside the very slender procambial cells.

Distal to the stelar histogen is a meristematic region three to six cells in diameter and two to four cells deep. From the derivatives of the peripheral cells of the upper layer or layers of this region the cortical cells are differentiated. From the derivatives of a lower layer of the same region is differentiated the single layer of epidermal cells which undergo no further periclinal divisions but divide only transversely and anticlinally. From the lowest layers of this meristematic region the root cap is differentiated. The cortex, epidermis, and root cap are first distinguishable as distinct regions at about equal distances from the center of the common histogen from which they are derived. One or two periclinal divisions of the cells of the region between the epidermis and stele give the cortex its mature width of from five to eight, usually six cells. The cortical cells have divided transversely more frequently than those of the stele and less frequently than those of the epidermis, and thus are intermediate in length between the two.

The root cap consists of several conical layers of cells of which the outer is oldest and largest. Near the apex of each cone the cells are larger, slightly more numerous, and elongated longitudinally, resulting in the wedge-shaped outline of the cap. At the center of the root cap, where there has been least distortion by growth, a longisection shows two to four somewhat irregular vertical rows of cells, each row still clearly traceable to a single cell of the histogen.

Vascular anatomy of cotyledon

Differentiation and maturation of xylem first begin above the slit and from this point proceed upward and downward at about equal rates. The protoxylem in the cotyledon, and other leaves as well, consists usually of spiral elements, although some annular thickenings may be present, especially in the tapering ends of the tracheids. In the cotyledon as seen in transection there is developed one protoxylem area and a band of metaxylem on each side of the younger part of this protoxylem. Eventually there is formed a stocky Y-shaped area of xylem with an accompanying area of phloem at the end of each upper arm of the Y (figs. 3-6). Sometimes

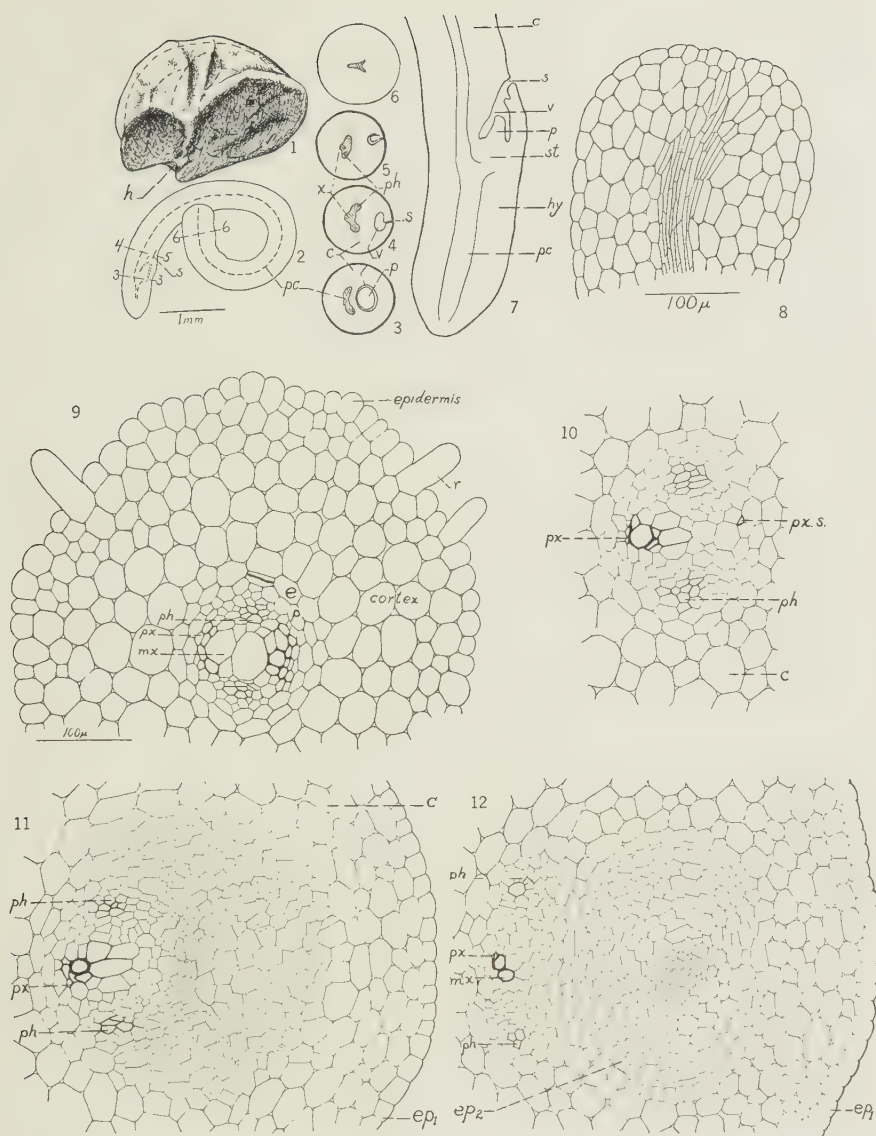
the xylem is separated into three or four groups by parenchyma, or the Y may be flattened like a short-stemmed T. Phloem matures first at the points farthest removed from the protoxylem.

In two seedlings, each with two growing points at the tip of the stem, there was only one cotyledon but two cavities, one for each growing point, and one vascular bundle in the cotyledon between the two cavities. The xylem of this bundle appeared in transection as an oblong band flanked on either side by a cavity with its growing point. The protoxylem was at the middle of one of the longer sides of the xylem area and a phloem group was at each of its ends. Thus in this case as well as normally development of the xylem was exarch. In one of the seedlings the primary root had four phloem groups and was probably tetrarch. The root of the other was not seen.

CHAUVEAUD (1) reports resorption of the protoxylem and its replacement *in situ* by metaxylem in the cotyledon of seedlings eight to ten days old. He figures ten transections but no longisections to show this. Actually no resorption occurs, but the protoxylem vessels become so stretched by the growth of the surrounding cells that their annular thickenings are so widely separated or their spiral elements so much stretched that the walls between thickenings collapse, and in transection the vessels are seen as only a very small patch of cellulose easily overlooked. This protoxylem becomes more difficult to find as the cotyledon becomes older. EAMES and MACDANIELS (3) report a similar situation in *Lobelia*. In longisection protoxylem is easily seen in all material less than four weeks old, at which age the second and third leaves have appeared and the cotyledon begins to wither from the tip downward toward its base. Development of the cotyledonary xylem is exarch throughout.

Anatomy of stem

In the germinating seedling all of the hypocotyl is rootlike in structure. Near the top of it the two protoxylem areas of the stele of the root appear rather abruptly, much separated from each other. The one extends into the cotyledon while the other ends at a distance equal to from one-third to one-half the diameter of the cotyledon beneath the primordium of the second leaf (fig. 7). The protoxylem of this latter strand is never extended up farther but ends blindly (fig. 10). Immediately above the level at which this protoxylem



FIGS. 1-12.—Fig. 1, seed showing position of embryo (drying of endosperm causes irregular wrinkling). Fig. 2, embryo dissected out of seed. Fig. 3, diagram of transection through embryo at level 3-3 of fig. 2. Figs. 4, 5, same, but at level 4-5, showing variation in structure at slit (*s*) and in outline of procambial strand (*pc*). Fig. 6, same, but at level 6-6. Fig. 7, diagram of longisection through portion of embryo. Fig. 8, longisection through tip of haustorium showing procambial cells extending to epidermis which is without a cuticle (*c*, cotyledon; *h*, hilum; *hy*, hypocotyl; *p*, leaf 2 primordium; *pc*, procambial strand; *ph*, position of future phloem; *s*, slit; *st*, stem; *v*, cavity in hollow base of cotyledon; *x*, position of future xylem). Fig. 9, transection through upper part of primary root of 6-day seedling. Fig. 10, transection 390μ above fig. 9, showing protoxylem under stem (*pxs*) consisting of single cell only. Fig. 11, transection 90μ above fig. 10, showing actively dividing cells of cortex (stippled) beginning formation of first adventitious roots. Fig. 12, transection 190μ above fig. 11, showing leaf 2 with first procambial strand (stippled) inside cotyledon (*c*, cortex; *e*, endodermis *ep*₁, epidermis of cotyledon; *ep*₂, same of second leaf; *mx*, metaxylem; *p*, pericycle; *ph*, phloem; *px*, protoxylem; *r*, root hair).

area ends, all of the xylem of the cotyledonary bundle and of the stem develops in one direction, away from the protoxylem of this cotyledonary bundle toward the center of the stem and even beyond it. At this level the four or five elements of the cotyledonary protoxylem are arranged side by side in a line which would pass perpendicularly to a radius of the stem extended through them. The metaxylem between this line of protoxylem and the point above the other protoxylem area appears in transection as a wedge-shaped area with two or three isolated metaxylem vessels at its point, but separated from the remainder of the metaxylem by parenchyma. Excluding the cotyledonary bundle, these isolated vessels are the first of the stem xylem to mature. Later at this level metaxylem matures on all sides of these isolated vessels, but at a slightly higher level, only on the side farthest from the cotyledonary protoxylem, that is, centrifugally. At the same time xylem matures also on each side of the metaxylem wedge as well as around its tip, but is separated from the wedge by a layer of parenchyma. Thus in transection there appears a thick **U** of xylem surrounding the wedge, except at its widest portion which is cotyledonary xylem. The base of this **U** is split off higher up to form the largest and central bundle of the second leaf. Part of the remaining arms form a portion of the two bundles of the second leaf, lateral to its largest bundle, and part continues upward to form the outer rather definite vascular layer of the stem (fig. 27). This outer layer, however, is formed largely from the steles of the adventitious roots.

The point at which parenchyma is first apparent in the upper hypocotyledonary xylem is arbitrarily called the bottom of the stem. In a seedling ten days old the stem is less than one-half as long as the diameter of the seedling and contains no matured xylem except the cotyledonary bundle. About ten more days are required for the first xylem to mature through this short length of stem up as far as the base of the second leaf. The lower part of this xylem consists of reticulate cells not more than three times as long as wide. The xylem slightly farther up is scalariform, while in the leaf the protoxylem is again of long spiral vessels which mature centrifugally.

In the center of the stem the vascular arrangement is determined largely by the manner in which the leaves develop. Each successive

leaf matures as an upright hollow cylinder, one side of which grows much more rapidly than the other, to form the blade, while the cylinder itself is the sheath surrounding the younger leaves and the apical meristem (figs. 24, 25). Because of the cylindrical sheath, therefore, the vertical vascular bundles of the leaf are arranged in a circle at its base. The largest bundle is near the center of the side forming the blade. The largest bundle of leaf 2 is farthest from the cotyledonary bundle and that of leaf 3 is near the cotyledonary bundle but separated from it by the sheath of leaf 2. In the stem the bases of the larger bundles of each leaf are connected with a horizontal U- or C-shaped ring of vascular tissue. Successively higher rings have vertical connections with each other, and thus a central parenchymatous area, the pith, is surrounded by a cylindrical network of vascular bundles. Lateral branchings extend from this central vascular cylinder toward the periphery of the stem, but are branched extensively both horizontally and vertically before they are anastomosed with the vascular layer limiting the stele. Over half of the stele is parenchymatous.

Leaf traces are never connected directly with the vascular tissue of the adventitious roots. The traces of larger bundles of the leaf are connected directly with the perimedullary vascular cylinder, while those of the smaller bundles are connected with the vascular tissue of the stem nearer its periphery. At the periphery of the stem the vascular tissue of the roots, with that of the outer stem, is spread out to form an almost continuous layer of intimately connected vascular bands outlining the stele of the stem. Leaf traces, as they pass through this layer of vascular tissue, are separated from it by parenchyma. The vascular connections of this peripheral layer with the perimedullary cylinder are never direct but irregular, and of such a nature that both soil minerals and organic foods may pass through a number of different routes to their destination. The bundles of the stem are for the most part amphivasal, with a layer or two of parenchyma separating the xylem and the phloem (fig. 27*B*). The amount of xylem on the side of the leaf trace farthest from the pith diminishes as the trace extends upward and outward, so that in the leaf the bundle is collateral.

A rather thick parenchymatous cortex penetrated by numerous

roots surrounds the stele. Since successive leaves touch each other, the stem is without an epidermis of its own. In longisection the stem appears somewhat heart-shaped, because successively formed parts have a greater diameter and because the apical meristem is increasing in size less rapidly than the surrounding area (fig. 27).

Adventitious roots

Adventitious roots originate very near the apical meristem of the stem and, because it is slightly sunken, at about the same level as this meristem (fig. 29). Their steles are continuous with that of the stem (fig. 28). Although the pericycle is not distinguishable as a single layer, it is in this region of the stem that the stele of the adventitious root originates. The cortex of the root appears continuous with the inner cortex of the stem. As the root elongates it first pushes through the outer cortical cells, which elongate somewhat during the process, and then through the bases of two or three fleshy sheaths. In so doing occasionally a root may penetrate the inner epidermis of a sheath but fail to pierce the outer. As a result the root usually grows upward for some distance through the mesophyll of the sheath, and finally dies when this becomes desiccated.

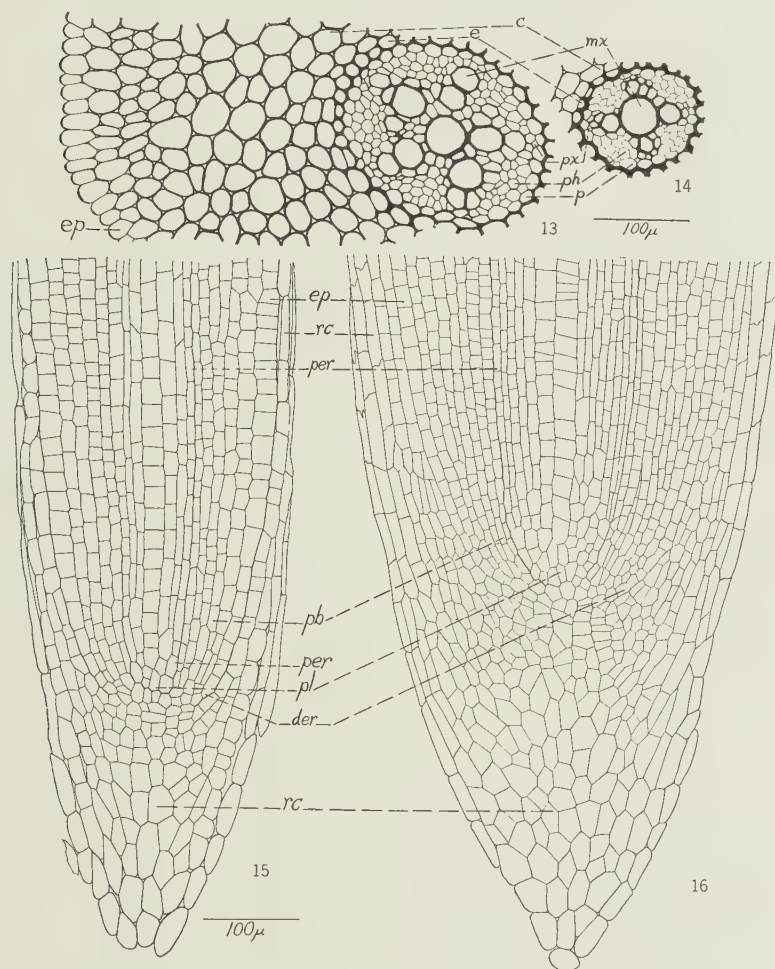
Development of the axis of the adventitious root proceeds exactly as in the primary root, except that in the former each region is larger because of a correspondingly greater number of cells (fig. 16). Tetrarch, pentarch, and hexarch steles occur on the same plant although the pentarch is most common (fig. 13).

In a mature root there is no space between the epidermis of its proximal part and the cortex of the stem through which it has broken (fig. 27). Adventitious roots may branch after they have attained a length of 10–15 cm. These branch roots break through the cortex and epidermis and usually occur on the convex side of the root. Older roots and leaves and older parts of the stem die and shrivel or disintegrate during the first year of a plant's development, thus making the bottom of the stem somewhat flat.

Development of leaf

The phyllotaxy of the onion is $1/2$. The apical meristem of the stem from which leaves are formed, and which eventually grows up

into the flower scape, is a low, circular, dome-shaped mass of cells (fig. 18). One side of this region (*c*, figs. 17, 18) grows up more rapidly than the center or axis (*e*) or than the opposite side (*b*), and owing to



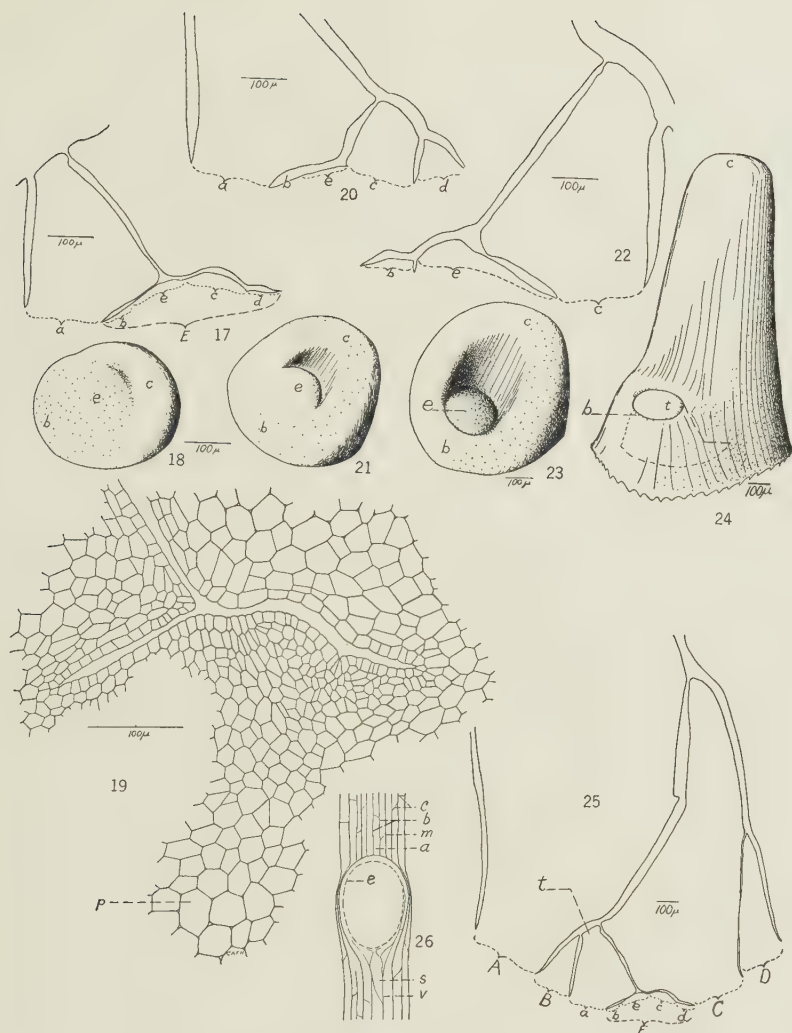
FIGS. 13-16.—Figs. 13, 14, transections of mature portions of adventitious roots: pentarch section (fig. 13) from portion of root near cortical region of stem; tetrarch (fig. 14) from portion 9 mm. distant from stem (*c*, cortical parenchyma; *p*, pericycle; *ph*, phloem; *px*, protoxylem). Fig. 15, median longisection of primary root grown in soil. Fig. 16, same of adventitious root grown in water (*der*, dermatogen; *ep*, epidermis; *pb*, periblem; *per*, pericycle; *pl*, plerome; *rc*, root cap).

centripetal growth as well, soon overgrows the axis (figs. 20-23). As the one side continues to grow higher, the entire periphery of the growing region begins to extend upward around the axis, from which there has now been differentiated the blade of the next leaf, which at this time is also growing at the same rate as the more slowly rising part of the periphery (figs. 24, 25). Thus the vertically oriented, hollow, cylindrical base of each leaf surrounds and incloses within itself the younger leaves and apical meristem. At maturity this cylindrical base of the leaf is the sheath or bulb-scale while the one elongated side is the blade. The rather angular shape of the younger leaves is determined by the surrounding structures, which limit and in a way mold the younger leaves within. During the differentiation into sheath and blade there is much rapid increase in the diameter of the growing region, so that the base of the newly formed leaf is pushed farther and farther away from the center (fig. 27). At the same time the thickness of the leaf blade and of the sheath continues to increase, so that by the time the next younger leaf is differentiated no more periclinal walls are formed. Further increase in the thickness of the sheath to form the fleshy bulb-scale is due to the formation and enlargement of intercellular spaces and to the growth of the cells.

The opening at the upper end of the sheath is designated, for convenience, the orifice of the sheath. A thin membrane extends around the upper edge of the orifice even on the side bearing the blade. Here the membrane is formed by an outgrowth, five or six cells thick, from the edge of the blade, and is usually without vascular tissue (figs. 27, 29).

In the first six or eight leaves elongation is proportionately greater than in later formed ones, and thus this orifice has become longitudinally much stretched so that its sides touch each other and close the cavity within until the next younger leaf is pushed through. In older leaves the tip of the blade is pushed through the orifice while both are inclosed within the sheath of the next older leaf.

In the formation of the first few leaves of a seedling, the blade attains a considerable length before the sheath begins to elongate appreciably. In a newly emerging leaf elongation takes place at about equal rates in all parts. The leaf tip is the first part to cease elongation, however, while the base of the sheath remains meristematic



FIGS. 17-26.—Fig. 17, longisection through stage shown in fig. 18; *a* and *d* are opposite sides of same leaf overgrowing the center (*bec*). Fig. 18, earliest stage of leaf differentiation. Fig. 19, cell detail of region *E* of figs. 17 and 25; plane of cell divisions marks boundary between regions *e* and *c*. Figs. 20, 21, one side (*c*) has outgrown the axis (*e*) and other side (*b*) and is beginning to overgrow it. Figs. 22, 23, both sides (*b* and *c*) overgrowing axis (*e*) which is itself beginning to extend upward. Corresponding parts have the same letters. Figs. 24, 25, the more rapidly growing side (*c*) has developed to form blade of leaf, whereas the upwardly growing periphery forms the sheath or bulb scale. (Small letters of first seven figures correspond to capitals in fig. 25.) *A* and *D*, *C* and *B*, and *a* and *d* are respectively the blade and the sheath sides of successively younger leaves (*p*, pith; *t*, tip of younger leaf). Fig. 26, arrangement of vascular bundles in mature leaf in region of leaf orifice (*a*, adaxial side of blade; *b*, branches from larger bundles; *c*, cross connections between adjacent vascular bundles; *e*, edge of orifice; *m*, bundle continuous in sheath and blade; *s*, outer side of sheath; *v*, bundles ending blindly under orifice).

longer than any other part. Thus in the earliest stage of development the entire leaf is meristematic; at a later date, only the sheath and base of the blade; and still later, only the base of the sheath. The lowest portion of a half-grown blade remains meristematic until the leaf is nearly grown, however, so that this region gives rise to a large share of the blade. Any one leaf, after it reaches a length of 3 cm., attains its mature length in a few days.

Mitosis continues in all parts of the leaf long after intercellular spaces appear (leaf *X* and younger, fig. 27). Transverse divisions as well as growth of the surrounding parenchymatous cells cause these spaces to become enlarged and elongated throughout the entire leaf. At the periphery of the blade in a very early stage of development there is differentiated what appears to be a meristematic layer (fig. 27). As the leaf elongates the cells of this layer do not become elongated longitudinally but radially, so that in the mature leaf they form two or three subepidermal layers of columnar cells corresponding to the palisade cells of dicotyledonous leaves. As these cells divide anticlinally they also increase the diameter of the blade. The inner parenchyma does not keep pace with increase in size, and so a huge central cavity which runs the entire length of the blade is torn through this inner spongy tissue. Before this cavity is formed all the inner cells of the leaf contain functional nuclei, although the volume of the intercellular space is probably greater than that occupied by the cells. After the cavity is torn the cells near its edge soon die, and so by their own collapse, according to NEWCOMBE (7), add to the size of the space. The mature leaf therefore consists of this central cavity, surrounded by eight or ten layers of parenchyma with large intercellular spaces, the vascular bundles, the palisade layers, and the epidermis.

Anatomy of leaf

Differentiation of leaf traces begins in the stem adjacent to its xylem, and proceeds upward into the developing leaf. In leaf blades which are no longer than they are thick (fourth younger leaf than *X*, fig. 27), procambial strands are already differentiated. Maturation of the bundles is endarch, beginning in the stem and, once begun in the leaf, proceeding upward rapidly to the tip. The first protoxy-

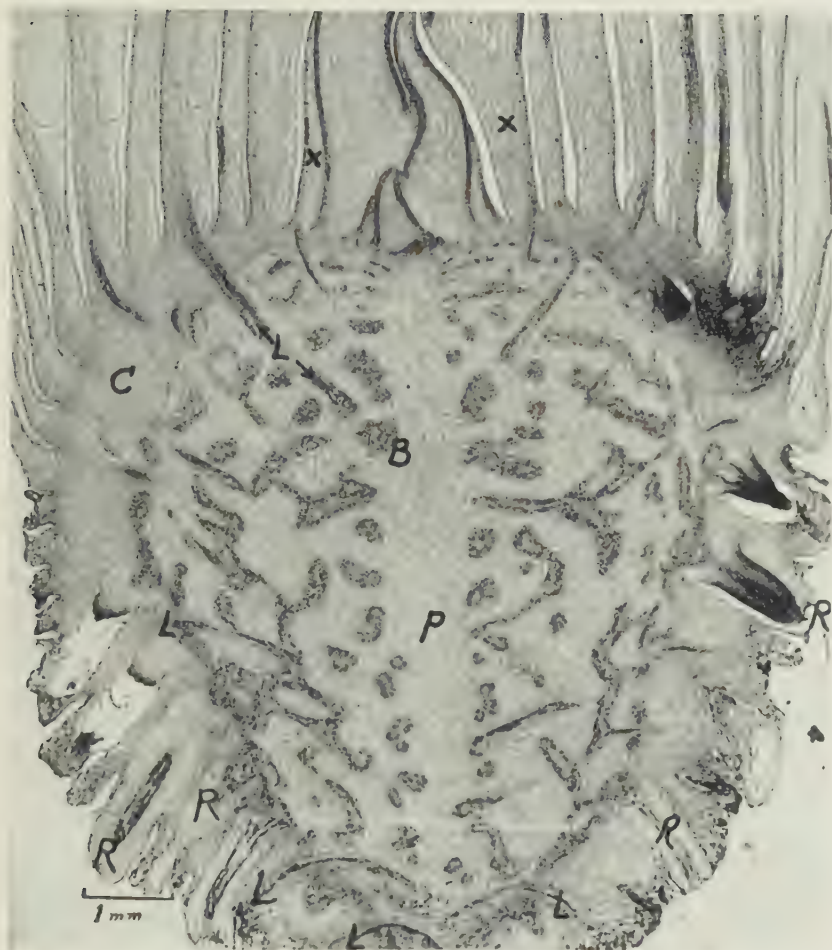
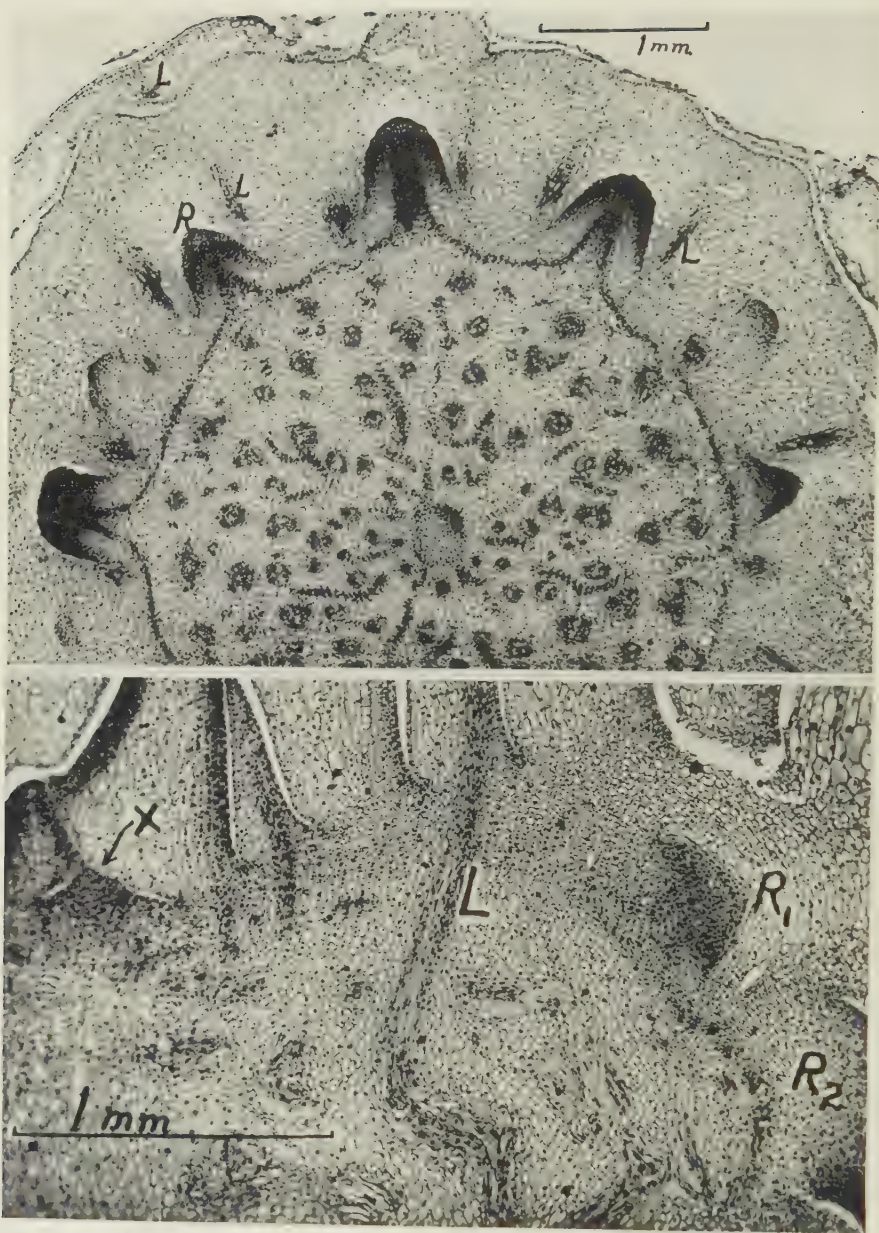


FIG. 27.—Median longisection, except at bottom, through plane of phyllotaxy of stem five months old; bulb development scanty, leaves 40 cm. long, and apical meristem at stage shown in fig. 21. Youngest five leaves contain mitotic figures. Row of dots in outer part of leaf *X* and of next older leaf are transections of connections between parallel leaf bundles. Darker tissue at edges of blades will become palisade tissue (*B*, transection through perimedullary bundle from which bundles of leaf arise directly; *C*, cortex; *P*, pith; *L*, vascular connections of leaf with stem; *R*, same of root with stem; *X*, sheath and blade of one leaf).



FIGS. 28, 29.—Fig. 28 (above), transection of stem five months old 50 μ below apical meristem. Procambial strands of four adventitious roots (R) are continuous with outer procambial tissue of stem. Plane of phyllotaxy is parallel to side of page. Bundles shown in transection are arranged in seven concentric circles or arcs, one for each leaf. Of the innermost leaves only bundles of blade are shown, bundles of sheath not yet being differentiated. Radiating procambial strands inside of stele connect vascular or procambial tissue of developing roots and of leaves (L , vascular bundles of leaf). Fig. 29 (below), longisection through apical meristem and roots (L , vascular bundle of sheath of leaf; R_1 , root primordium; R_2 , older root; X , apical meristem).

lem is matured throughout the entire length of the leaf before any metaxylem is differentiated. Practically all of the xylem consists of spiral elements.

The cotyledon has only one vascular bundle; the second leaf has five; the next has usually eight; and successively older leaves may have one or two more bundles than the preceding leaf, until in the sheath of a mature bulb there are often as many as forty. These bundles are arranged around the periphery, run parallel throughout its entire length, and usually retain their individuality in spite of rather frequent small branchings and cross connections. These cross connections originate in one or several rows of parenchymatous cells which lie adjacent to and between the bundles. The cells divide at various angles periclinally and transversely to form many smaller cells which mature as a cross connection (fig. 27).

In both sheath and blade smaller and larger bundles may originate blindly or their bases may be anastomosed with larger bundles. Some of the smaller ones end blindly near the base of the blade. In the outer sheaths of a mature bulb there are very few cross connections between adjacent vascular bundles in the lower half, but many in the upper. There are cross connections at all levels in the unthickened sheath of a young onion. In outer sheaths of bulbs the vascular bundles often appear green because here a layer of subepidermal chlorenchyma almost surrounds them.

In a mature leaf the circular orifice of a young sheath has become oval and appears laterally placed, owing to a greater elongation of the sheath on the side bearing the blade. Near the base of the sheath vascular bundles are rather uniformly distributed, but near its top the bundles are more closely crowded together on the side from which the blade develops than on the opposite side. In the middle of this latter side are one or two smaller bundles which, after several branchings and cross connections, end blindly under or around the upper margin of the sheath. On each side of these is a larger bundle which parallels them up to the orifice and then is curved so as to parallel its edge. At the base of the blade these two bundles are again vertically oriented, making a sharp angle with their former course around the edge of the orifice. From this angle a smaller branch is continued around the periphery of the orifice

until, near the middle of the base of the blade, it meets a like branch from the other side. At the junction of these two a vertical bundle extends upward into the blade. Between this vertical bundle and each of the original large bundles is usually one other bundle extending upward from the branch around the top of the orifice. Frequently also the original large bundles have a vertical branch extending into the blade before they themselves become vertically reoriented. On either side of these two main bundles, the other bundles of the sheath are crowded together more closely near the sides of the orifice, but again acquire a uniform peripheral distribution in the blade (fig. 26).

In the cotyledon and in all subsequent leaves there occur longitudinal rows of elongated cells situated usually two cell layers beneath the epidermis. These are rows of lactiferous cells which are filled with a whitish fluid containing, according to RENDLE (9), resins and a substance easily hydrolyzed to allyl sulphide. It is this milky liquid which gives the broken onion tissue its characteristic taste and smell. The lactiferous cells in a longisection of a cotyledon 14 days old are easily recognizable, since they stain differently from the surrounding cells, are several times longer, and contain proportionately longer nuclei. In older leaves they occur just within the chlorenchymatous layers also. Their position has no relation to that of the vascular bundles. RENDLE believes that they probably perform either an excretory or a protective function, or both.

Stomata are numerous on the cotyledon of a seedling less than a week old. An epidermal cell and the two guard cells at one end of it were originally one cell. In the development of the stoma, this one cell, instead of dividing near its center as previously, divides at one end, cutting off a characteristically long epidermal cell and a square cell. This cell by one longitudinal division forms two cells which, as soon as the stoma between them is formed, become its guard cells. In a mature leaf the guard cells are sunken beneath the remainder of the leaf surface by more than their own thickness and the adjacent epidermal cells have overgrown them. The cuticle on the exposed epidermal cells is half as thick as the diameter of their own lumen. The surface of the leaf is glabrous and slightly glaucous.

Bulb

The onion bulb consists of a very short stem bearing adventitious roots and a series of thickened leaves and leaf sheaths, the older surrounding the younger, which have at their center still younger leaves and usually several apical meristems. The blades of the leaves may be functional, dried down, or, in the older of the inner leaves, undeveloped. In a large mature bulb the functional blades of the outer six or seven leaves have become dried and broken off, leaving only the sheaths. The outer of these sheaths have themselves also become dried and form a protection for the fleshy storage leaves within. Inside are three or four leaves with very short undeveloped but usually green blades, and inside these are successively younger leaves with blades proportionately longer as the leaves are younger and smaller. In the spring it is these youngest leaves that continue development and become green. The storage leaves outside of them also elongate, especially their sheaths, but their green blades remain relatively small. As the inner and younger leaves grow, the outer fleshy storage leaves become progressively dry from the top of the sheath to its base, because of withdrawal of stored food and moisture. Before leaf growth occurs, however, numerous roots are developed from the periphery of the stem. These extend into the soil and absorb moisture for this whole process.

The time at which formation of the bulb may be initiated varies. A bulb 1 cm. in diameter may be formed when only the fourth leaf shows, or eight or ten leaves may be formed before there is any evidence of thickening of the sheaths. In the first case the food which is being manufactured is stored, while in the second it is used in the formation of more and larger leaves. These two extremes may occur in plants growing under almost identical conditions.

Summary

1. The structure of the embryo and development of the seedling of *Allium cepa* are described.
2. The primary root is diarch. In its growing point are two histogens, the inner giving rise to the stele and the outer to the remainder of the root.

3. The adventitious root is usually pentarch, originates in the pericyclic region of the stem at the level of the apical meristem, and develops in a manner similar to that of the primary root. Secondary roots may be developed from the adventitious roots.

4. The first vascular tissue to mature is in the cotyledon. Xylem matures centripetally throughout this structure.

5. Transition from an exarch to an endarch condition of the xylem in the lower part of the stem is described.

6. The stem consists of a parenchymatous cortex, a stele which contains branched and anastomosed amphivasal vascular bundles in a groundwork of parenchyma, and a central pith surrounded by a cylindrical network of bundles to which most of the leaf traces are connected.

7. The development of the leaf is described. Vascular bundles of the leaf parallel each other, connect at frequent intervals, and are situated near the periphery of the leaf. The formation of guard cells and stomata is described.

8. Longitudinal rows of lactiferous cells are near the surface of the leaf but without relation to the vascular bundles. These rows never form vessels.

9. The structure of an onion bulb is described.

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